PROC. BIOL. SOC. WASH.
106(4), 1993, pp. 645–660

OCTOPUS ORNATUS GOULD, 1852 (CEPHALOPODA: OCTOPODIDAE) IN AUSTRALIAN WATERS: MORPHOLOGY, DISTRIBUTION, AND LIFE HISTORY

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Abstract.—The morphology, distribution, and life history of the "white-striped octopus," *Octopus ornatus* Gould, 1852, from Australian waters are reported. Information gathered on habitat preferences, activity patterns, foraging behavior and diet also are presented. Australian representatives of this species are described and compared with the neotype from Hawaiian waters. Prior reports of *O. ornatus* from Australia refer to a related species, *Octopus aspilosomatis* Norman, 1993a. Distributional records from Asia, the Indian Ocean and the South Pacific Ocean are presented. The known distribution of *O. ornatus* extends from Easter Island and the Hawaiian islands, west to eastern Africa. Delineation of *O. ornatus* from related taxa is discussed.

The "white-striped octopus," *Octopus ornatus* Gould, 1852, is a large, nocturnally-active octopus found primarily in association with coral reefs throughout the tropical Indian and West Pacific Oceans. This species originally was described by Gould (1852) on the basis of specimens from the Hawaiian Islands collected on the Wilkes U.S. Exploring Expedition of 1838–1842. Original type material has never been traced and is presumed lost (Voss 1981). Voss (1981) redescribed the species and designated a neotype from Oahu Island, Hawaii (93.7 mm ML male, USNM 730020). Voss also described additional specimens from Hawaii, the Marshall Islands and Kenya, and synonymized *Callistoctopus arakawai* Taki, 1964 from southern Japanese waters.

Octopus ornatus was reported from Lizard Island at the northern end of the Great Barrier Reef, Australia by Roper & Hochberg (1987, 1988). Specimens and photographs of the taxon referred to in these works have been re-examined and proved to belong to a distinct species, *Octopus aspilosomatis* Norman, 1993a.

This paper presents the first record of the true *O. ornatus* from Australian waters. A detailed description of the Australian specimens and a comparison with the neotype are provided. Additional counts and indices from the neotype are provided beyond those included in Voss's (1981) treatment. This species is reported for the first time from a number of new localities in the Pacific and Indian Oceans. Observations of live *O. ornatus* from Australia provide some information on habitat preferences, foraging behavior, diet and activity patterns.

Methods

Nine live *O. ornatus* were encountered in the field in two visits to One Tree Island, Capricorn Bunker Group, southern Great Barrier Reef in October 1989 and September 1990. Individual animals were observed and photographed in situ. Seven animals were collected and returned to aquaria where they were observed, described and photographed. The seven specimens were killed in fresh water, fixed in 10% formalin for a

minimum of two weeks and preserved in 70% ethanol, according to the techniques of Roper & Sweeney (1983). This material is now housed in the Museum of Victoria, Melbourne, Australia. Voss's neotype of *O. ornatus* was examined in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. A total of 39 additional preserved specimens were examined in the collections of the Museum of Victoria, Melbourne, Australia (NMV), Australian Museum, Sydney, Australia (AMS), Santa Barbara Museum of Natural History (SBMNH), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), California Academy of Sciences, San Francisco, California (CASIZ), British Museum (Natural History), London, England (BMNH) and Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Field collection at Lizard Island, northern Great Barrier Reef, in November 1989 enabled observation and collection of *O. aspilosomatis* Norman, 1993a, the species referred to as *O. ornatus* by Roper & Hochberg (1987, 1988). Specimens from Lizard Island treated in these works were examined at the Smithsonian Institution, Washington, D.C. in June 1990.

In the description and tables, measurements and indices follow Roper & Voss (1983:56) and Toll (1988). The following additional or modified indices and symbols also are employed:

Arm Mantle Index (AMI): arm length as % of ML; Arm Width Index (AWI): arm width at widest point on stoutest arm, as % of ML; Free Funnel Index (FFI): length of free funnel portion as % of funnel length; Funnel Length Index (FLI): funnel length as % of ML; Funnel Organ Index (FOI): length of outer limb of funnel organ as % of medial limb length; Funnel Organ Length Index (FOLI): length of medial limb as % of funnel length; Gill Count (GC): number of gill lamellae per demibranch not including the terminal lamella; Head Mantle Index (HMI): head width as % of mantle width; Hectocotylized Arm Mantle Index (HAMI): length of hectocotylized arm as % of ML; Spermatophore number (SpN): number of spermatophores in Needham's Sac; Stage of Maturity (StM): Immature (Imm: sex indeterminate or reproductive organs minute), Submature (S: reproductive organs distinct but poorly developed) and Mature (M: developed spermatophores or eggs distinct); Sucker Count (SC): number of suckers on arm with highest sucker count.

Family Octopodidae d'Orbigny, 1839
Subfamily Octopodinae d'Orbigny, 1839
Octopus ornatus Gould, 1852
Figs. 1–5

Octopus ornatus Gould, 1852:476, fig. 590, 590a.—Gould, 1862:232.—Tryon, 1879: 112, pl. 30, figs. 29–30.—Hoyle, 1886a: 11; Hoyle, 1886b:220.—Robson, 1929: 108.—Boone, 1938:357, pl. 151.—Adam, 1941:9, 14.—Van Heukelem, 1966.—Voss, 1981:525, figs. 1–3, tables 1, 2.—Houck, 1982:152.—Nesis, 1982:74, plate (in 1987 translation).—Young, Harman & Hochberg, 1989:152, figs. 3, 5.—O'Shea, 1990:41, fig. 2.

Polypus ornatus.—Berry, 1909:418; Berry, 1914:294, pl. XLVI, figs. 1–2, textfig. 14.

Callistoctopus arakawai Taki, 1964:292, pls. 2–3, textfigs. 34–41.—Taki, 1965:324, textfig.; Taki, 1981:253.—Okutani, Tagawa & Horikawa, 1987:168, textfigs. 66A, B.

Octopus arakawai.—Dong, 1979:72, pl. 1, fig. 2; 1987:186, fig. 123.

Holotype.—Not extant.

Holotype locality.—Sandwich Islands (=Hawaiian Islands).

Neotype.—93.7 mm ML male (USNM 730020), designated by Voss (1981).

Neotype locality.—Pacific Ocean, Hawaii, Oahu Island, Black Point.

Material examined.—See appendix.

Diagnosis.—Medium to large nocturnally-active species with distinctive color pat-

tern of buff or white longitudinal stripes on dorsal and lateral mantle, in distinct contrast to a background of red brown or dark maroon red. Regular paired white spots on dorsal arm crown and along aboral surfaces of all arms. Interbrachial, lateral face of all dorsal suckers with large buff or white spot. Arms elongate (AMI 544.6–838.6), unequal in length, dorsal pair longest, grading to ventral pair shortest (AF 1.2.3.4). Webs shallow (WDI 5.3–11.3), dorsal web deepest (WF typically A.B.C.D.E). More than 300 suckers per arm in submature and mature animals. Hectocotylized arm with 150–180 suckers in submature to mature individuals. Large conical ligula in mature males (LLI 4.3–5.7). Eggs small, capsule up to 3.5 mm long. Gills with 13–14 lamellae per demibranch.

Description.—Counts and indices for the neotype and Australian specimens are presented in Tables 1 and 2. In the following text, the values for both the neotype and Australian material are given in brackets. The first number refers to the neotype, followed by the range and mean (underlined) in the Australian material. Voss (1981) reported that *O. ornatus* shows considerable variation in elongation of the mantle on preservation. A similar range was observed in the Australian material.

Medium to large species with elongate arms (Figs. 1a, 4a); ML to at least 100 mm for males and 130 mm for females; TL to at least 1200 mm; weight to at least 1000 g. Mantle shape variable, from ovoid to greatly elongated (Voss 1981, fig. 1b–d: MWI 76.6; 41.5–65.2–76.3). Mantle walls thick, muscular. Stylets present, poorly developed. Pallial aperture moderately wide, approximately half mantle width. Funnel broad-based and muscular (FLI 49.9; 37.0–47.9–59.7), free portion variable in length, approximately half funnel length (FFI 44.1; 31.1–49.5–69.4). Funnel organ well developed with broad limbs (Fig. 1b), outer limbs slightly shorter than median ones (FOI 85.6; 76.4–82.1–86.3). Funnel organ approximately 70% of funnel length (FOLI 80.3; 62.1–70.6–77.5).

Head slightly narrower than mantle (HWI 52.7; 27.3–46.8–56.4, gravid ♀: 37.3; HMI 68.8; 65.2–76.1–87.6), neck distinct, slightly narrower than head. Eyes medium-sized, slightly pronounced.

Arms long, typically 6–8 times mantle length (AMI 685.2; 544.6–688.1–838.6), moderately robust (AWI 23.9; 16.4–18.5–19.9), sub-cylindrical along length. Arm loss and regeneration evident at different levels along arms, on at least some arms in most specimens. Arms decrease in length and diameter from dorsal to ventral pairs, dorsal arms longest and most robust (AF 1.2.3.4). Suckers moderately large (SDI 14.0; 7.3–11.3–14.4), larger on dorsal arms; distinctly enlarged suckers absent in both sexes. Suckers moderately cylindrical with thick, muscular rims. Sucker rims finely scalloped, more pronounced in smaller distal suckers. More than 300 suckers on each intact arm in submature and mature specimens, females with slightly higher sucker counts (SC neotype R2: 378; R4: 400; SC ♂: 324–342–366, $n = 5$; SC ♀: 376, 382, $n = 2$). Webs shallow (WDI 7.8; 5.3–8.7–11.3), depths subequal, decreasing slightly from dorsal to ventral webs (WF typically A.B.C.D.E or A = B = C.D.E). Web margins extend as narrow retractile membranes on dorso-lateral and ventro-lateral edges for at least 70% of length of all arms.

Third right arm of males hectocotylized, short (HAMI 307.4; 253.9–310.2–353.6), approximately 60% length of opposite arm (OAI 84.7; 54.8–62.6–68.5). Ligula moderate sized in mature males (LLI 5.7; range for larger submature and mature Australian specimens: 4.3–4.9–5.6, $n = 4$), robust and cylindrical, tapering to blunt point (Fig. 1c). Ligula groove deep and usually closed. Calamus small but distinct (CLI 18.4; 13.6–15.3–18.4, $n = 4$). Spermatophore groove well developed, wide and thin with fine transverse ridges. Spermatophore guide distinct, bordered by flattened papillae or digits

Table 1.—*Octopus ornatus* Gould, 1852. Counts and indices for the neotype and males from Australian waters. (S = submature; M = mature; D = damaged; — = not recorded; ID = indistinct; R = regenerating).

Museum: reg. no.:	NMV F57920	AMS C115738	NMV F57921	AMS C115737	NMV F57923	NMV F57924	NMV F57918	USNM 730020 Neotype
ML	45.9	75.7	83.2	97.1	102.8	103.5	104.2	93.7
TL	394	638	668	750	727	688	≫582	754
StM	S	S	S	M	S	M	M	M
MWI	76.3	41.5	64.4	62.4	67.3	71.6	60.7	76.6
HWI	55.8	29.7	56.4	40.7	54.2	50.2	50.5	52.7
HMI	73.1	71.6	87.6	65.2	80.5	70.1	83.2	68.8
AMI:1	738.6	723.9	670.7	655.0	576.8	D	D	685.2
2	655.8	591.8	508.4	654.0	D	546.9	D	639.3
3	573.0	482.2	D	557.2	393.0	D	D	362.9R
H	313.7	330.3	330.5	120.5D	253.9	353.6	279.3	307.4
4	516.3	449.1	D	453.1	365.8	495.7	443.4	474.9
AWI	18.3	—	19.4	—	19.7	19.9	17.7	23.9
SDIn	12.6	7.3	14.4	10.9	13.5	11.5	9.2	14.0
SC	331	—	324	—	339	366	352	400
WDI	6.6	5.3	9.1	11.3	11.1	<12D	D	7.8
WF	A = B = C.D.E	B.A = C = D.E	A.B.C = D.E	A.B.C.D = E	A = B = C = D.E	A = B.C.D.E	ID	A = B = C.D.E
GC	14	13	13	13	14	13	13/14	14
HAMI	313.7	330.3	330.5	120.5D	253.9	353.6	279.3	307.4
OAI	54.8	68.5	D	D	64.6	D	D	84.7R
HASC	153	165	152	89D	169	172	164	163
LLI	2.8	1.3	4.3	6.3D	5.6	4.4	5.4	5.7
CLI	40.0	31.3	13.6	18.9D	15.8	18.4	13.3	18.4
PLI	13.1	12.5	11.7	16.9	15.5	10.0	15.4	9.4
SpLI				—		48.3, 49.3	38.4, 48.9	D
SpWI				—		2.2, 2.4	—	D
SpRI				—		44.0, 45.1	—	D
SpN				—		8	9	4
FLI	59.7	37.0	49.4	49.0	44.6	49.8	44.4	49.9
FFI	55.4	47.8	50.4	39.0	61.4	31.1	69.4	44.1
FOI	80.1	76.4	81.9	84.2	ID	83.0	81.6	85.6
FOLI	64.2	65.0	76.6	77.3	ID	77.5	69.3	80.3

Table 2.—*Octopus ornatus* Gould, 1852: Counts and indices for females from Australian waters. (S = submature; M = mature; D = damaged; — = not recorded; ID = indistinct; * = mature ovarian eggs only; G = distended gravid female).

Museum: Reg. no.:	NMV F57919	NMV F57922	AMS C169234
ML	77.3	83.5	132.0
StM	S	S	M
TL	512	738	1210
MWI	65.8	68.7	73.2
HWI	48.0	55.6	27.3
HMI	72.9	80.9	37.3G
ALI:1	544.6	756.9	838.6
2	469.6	638.3	582.6
3	410.1	540.1	575.0
4	388.1	479.0	502.3
AWI	16.4	18.1	—
SDIn	9.7	12.3	11.5
SC	382	376	—
WDI	8.9	8.5	8.9
WF	A.B. = C.D.E	B.C = D.E	C.B.D.E.A
GC	14	13	13
ELI*			2.7
EWI*			0.5
EN*			~35,000
FLI	41.7	51.3	52.1
FFI	45.6	46.2	48.4
FOI	83.5	86.3	ID
FOLI	62.1	73.1	ID

of skin. Approximately 160 suckers on hectocotylized arm (HASC 163; 152–164–172).

Gills with 13–14 lamellae (holotype: 14) on both inner and outer demibranchs, plus terminal lamella.

Digestive tract illustrated in Fig. 2a. Posterior salivary glands large (up to twice length of buccal mass), attached to lateral edges of crop diverticulum. Crop diverticulum well developed. Stomach bipartite. Caecum coiled to form 1.5 whorls, distinctly striated. Digestive gland elongate, approximately conical in shape and bilobed at posterior end. Intestine long, moderately narrow with a reflexed bend approximately one third from proximal end. Walls of rectum muscular in distal quarter of intestinal tract. Ink sac well developed, partially embedded in ventral surface of digestive gland. Anal flaps present.

Beaks illustrated in Fig. 2b–d. Upper beak with a short hooked rostrum and narrow hood (Fig. 2b). Lower beak with moderately sharp rostrum, narrow hood, widely spread wings and flared lateral walls separated in posterior half (Fig. 2c, d). Radula with seven teeth and two marginal plates in each transverse row (Fig. 4f, i). Rhachidian tooth with 2–3 lateral cusps, typically 3, on each side of large medial cone. Lateral cusps in symmetrical seriation, migrating from lateral to medial position over 9–10 transverse rows.

Male genitalia illustrated in Fig. 3. Penis in mature males of moderate size (PLI 9.4; in larger submature and mature Australian specimens 10.0–13.9–16.9, n = 5), genital aperture subterminal. Holotype contained damaged spermatophores. Spermatophores short (SpLI neotype: D; Australian material: 38.4–49.3, n = 4) and narrow (SpWI neotype: D; Australian material: 2.0–2.5, n = 4), apparently produced in low numbers (4 in Needham's Sac of holotype; 8 and 9 in two other males, NMV F57918, NMV

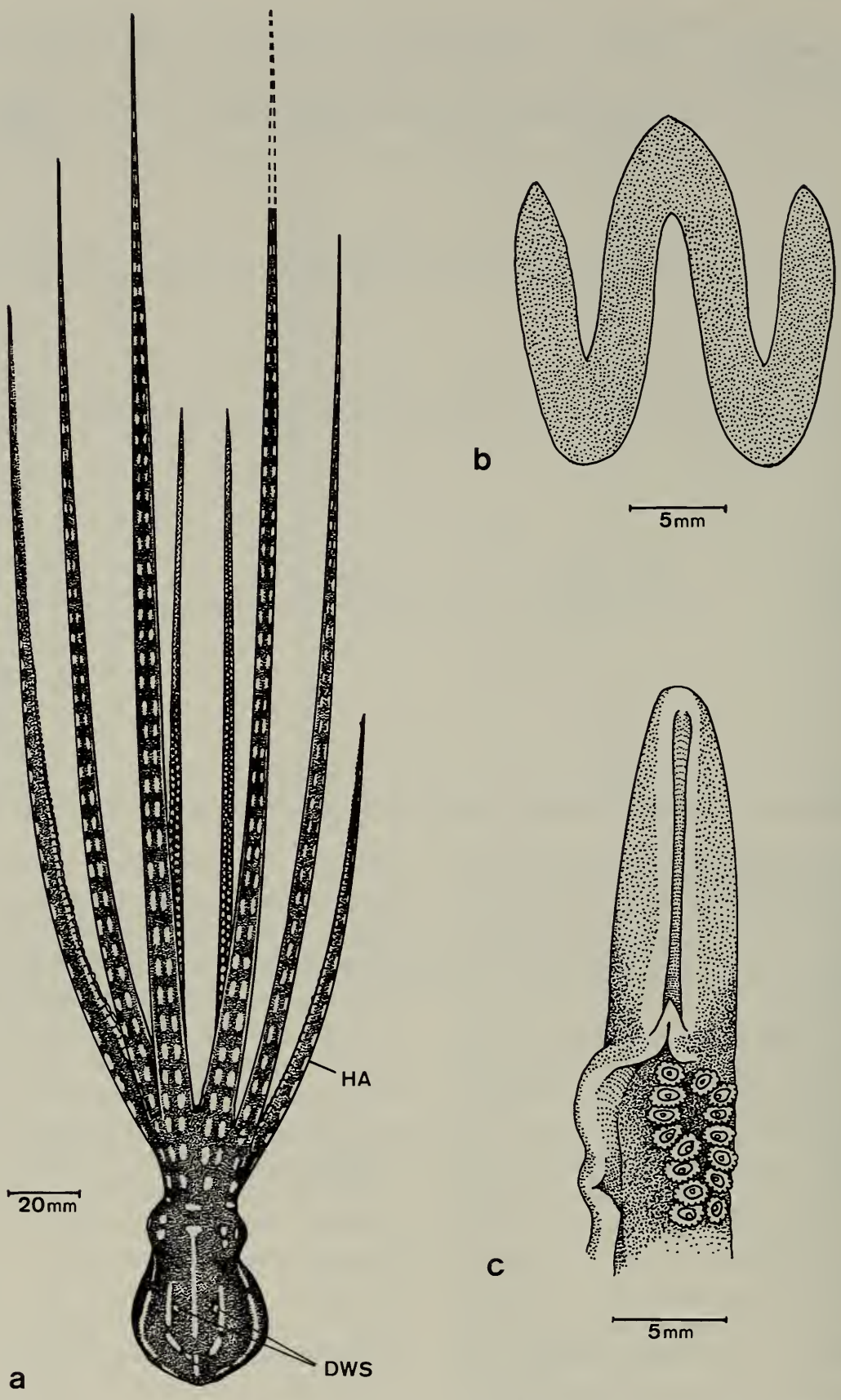

Fig. 1. *Octopus ornatus* Gould, 1852. a, Dorsal view of NMV F57920 (45.9 mm ML ♂), Abbreviations DWS = dorsal white spots, HA = hectocotylized arm; b, Funnel organ of same specimen; c, Hectocotylus of NMV F57918 (104.2 mm ML ♂).

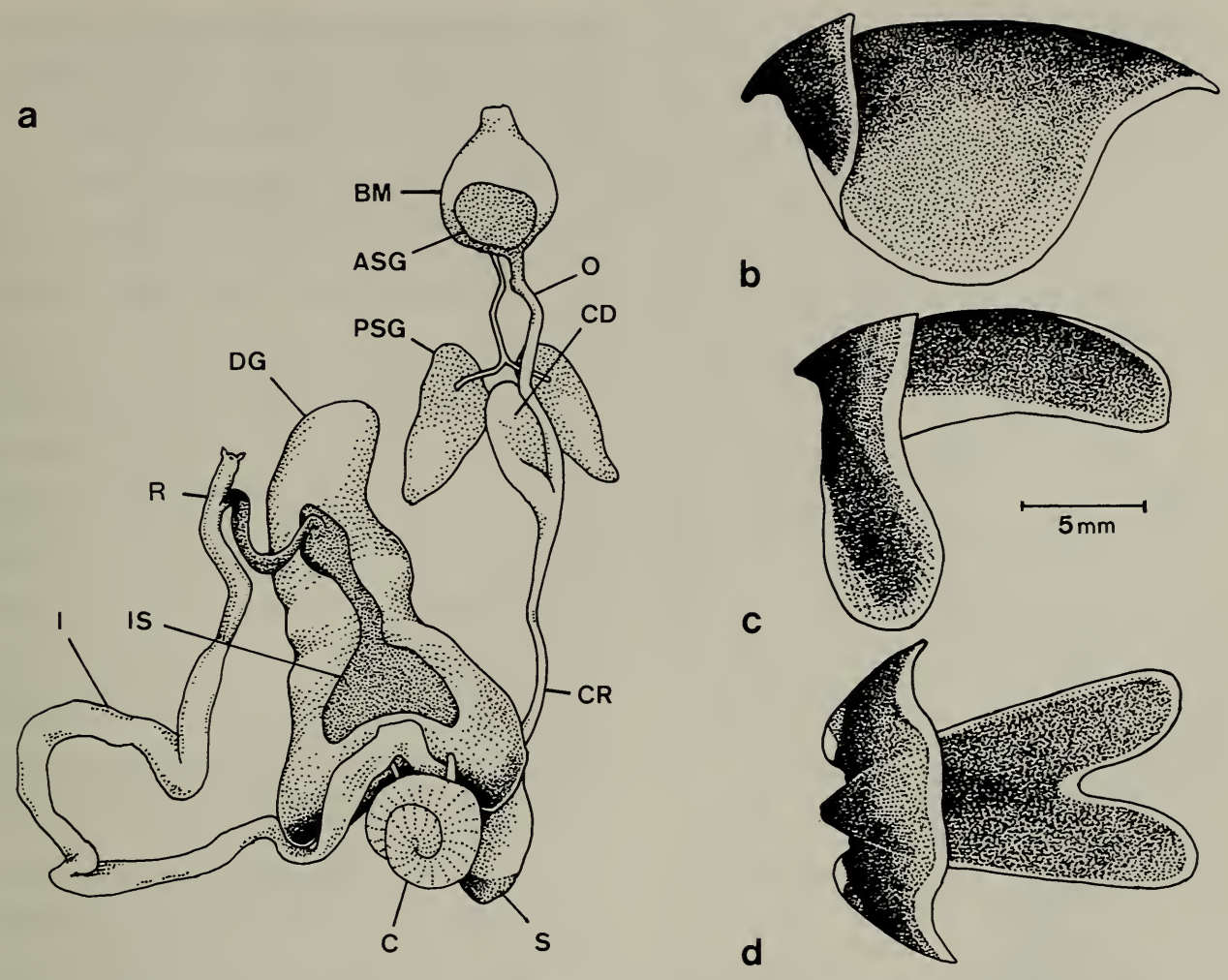

Fig. 2. *Octopus ornatus* Gould, 1852. a, Digestive tract from NMV F57922 (83.5 mm ML ♀), Abbreviations ASG = anterior salivary glands, BM = buccal mass, C = caecum, CD = crop diverticulum, CR = crop, DG = digestive gland, I = intestine, IS = ink sac, O = oesophagus, PSG = posterior salivary glands, R = rectum, S = stomach; b–d Beaks from NMV F57918 (104.2 mm ML ♂), b, Upper beak, lateral view; c, Lower beak, lateral view; d, Lower beak, ventral view.

F57924). Oral cap simple with long cap thread. Details of ejaculatory organ, cement body and sperm reservoir unclear in material examined due to poor preservation. Sperm reservoir approximately half total length (SpRI 44.0, 45.1).

Only one gravid female encountered in specimens examined (132.0 mm ML; AMS 169234). Mature ovarian eggs small, capsule length to 3.5 mm long (EgLI: 2.7; EgWI: 0.5); produced in large numbers (approximately 35,000 in ovary of above specimen). Oviducal glands partitioned into approximately 20 radiating chambers in gravid female and one submature female (1 ♀: 83.5 mm ML, NMV 57922).

Body coloration relatively fixed. Base color generally orange or red brown with distinctive series of buff or white stripes and spots on arms, dorsal body and bases of dorsal suckers (Figs. 1a, 4a–e, g, h). Pair of small dorsal white spots are visible on dorsal mantle when longitudinal stripes are suppressed (DWS in Fig. 1a; see also Fig. 4d, g). In alarm display, base color becomes deep maroon red with pure white stripes and spots (Fig. 4a, b, g). During daylight hours the base color in "inactive" animals light pink or gray, iridocytes evident as iridescent green hue.

Skin covered with small fixed patches separated by fine grooves to form an irreg-

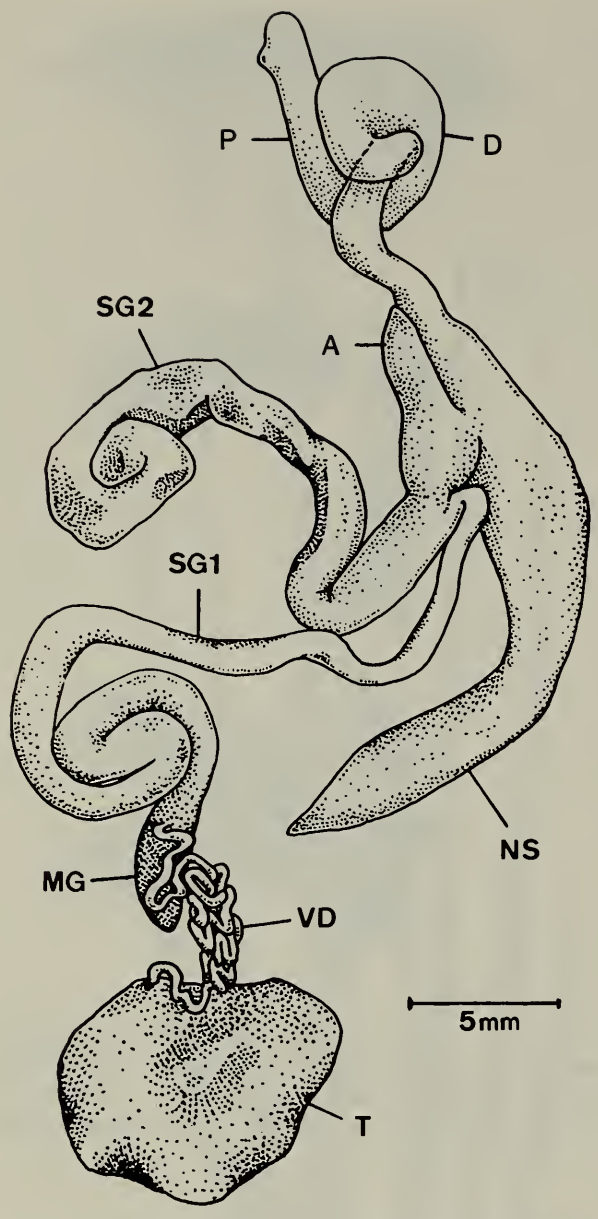

Fig. 3. *Octopus ornatus* Gould, 1852. Male reproductive tract from NMV F57918 (104.2 mm ML ♂). Abbreviations A = appendix, D = diverticulum, MG = mucilaginous gland, NS = Needham's sac, P = penis, SG1 = spermatophoric gland 1, SG2 = spermatophoric gland 2, T = testis, VD = vas deferens.

ular reticulation over all dorsal surfaces (Fig. 4d). Two moderate-sized papillae present over each eye (Fig. 4d). In alarm displays, longitudinal truncate flaps or ridges raised in centers of white stripes and spots (Fig. 4c–e).

Remarks.—The distinctive color pattern and sculpture of this species are typically visible in preserved specimens (Fig. 4h), enabling easy identification.

Sexual dimorphism is not marked in *O. ornatus*. Based on the few mature specimens available, females appear to reach a larger size than males. Additional material should be examined to confirm these trends.

Distribution.—In Australian waters, *O. ornatus* is reported from One Tree Island at the southern end of the Great Barrier Reef and on the New South Wales coast south to Sydney.

The known distribution of this species is considerably expanded here. *Octopus ornatus* is reported for the first time from: 1) the South Pacific: Easter Island, Society Islands (Tahiti and Raiatea), Cook Islands (Raratonga) and Fiji Islands (Rotuma and Vatao Island); 2) the West Pacific: Philippines (Batan Island), New Caledonia (confirmed from video footage of G. Boucher, MNHN); and 3) the Indian Ocean: Madagascar, Aldabra Atoll (West Island), Chagos Archipelago (Eagle Island), Reunion Island and the Seychelles.

Octopus ornatus thus is widely distributed in tropical waters of the Indian and Western and Central Pacific oceans (Fig. 5). It is reported from Hawaii and Easter Island in the east, through the Pacific Islands to Asia and Australia, and into the Indian Ocean to East Africa. Taki (1964, 1965, 1981) reported this species from southern Japan under the name *Callistoctopus arakawai.* Okutani, Tagawa & Horikawa (1987) also used this name for *O. ornatus* from the Okinawa Islands, in tropical waters south of Japan. Nishimura (1992) contains an illustration of *O. ornatus* from the Bonin Islands, also in tropical waters south of Japan.

O'Shea (1990) reported *O. ornatus* from New Zealand on the basis of a single female specimen. O'Shea illustrated the specimen (O'Shea 1990, fig. 2), which clearly is *O. ornatus,* providing the collection locality as "NZOI Station K23." Additional locality details have since been obtained. This specimen was collected from the Tonga Islands (18°41.70′S, 173°57.40′W) and, hence, does not constitute a record of this species from New Zealand waters.

Life history.—All nine *O. ornatus* encountered in the field were found on One Tree Island at the southern end of the Great Barrier Reef. One Tree Island is a true coral island formed within a large shallow lagoon. All *O. ornatus* were found within the lagoon during night low tides between 1930 and 0430 hr, active over coral rubble substratum in shallow water (0.2–2 m deep). Most specimens were foraging along the water's edge adjacent to exposed intertidal reef flats. Several individuals were encountered in openings of large lairs. These lairs consisted of deep vertical holes excavated in coral rubble. One specimen retreated into its lair and blocked the entrance at several levels with large pieces of dead coral. No evidence of *O. ornatus* lairs could be found during daylight hours, the entrances sealed with rubble during the day. It is unknown whether this species occupies permanent lairs or temporary/short-term refuges.

Individuals foraged over coral rubble, exploring burrows and holes with the dorsal arms, using tactile detection of prey. One specimen was caught carrying four alpheid shrimps on the proximal suckers of the lateral arms. A large captive individual of *O. ornatus* was observed to attack and commence devouring a small individual of another octopus species, *Octopus alpheus* Norman, 1993a. The intestine of another specimen (83.5 mm ML female, NMV F57922) contained the nearly intact upper and lower beak of an octopus, plus broken portions of other octopod beaks. No prey remains were found in middens around the entrance to lairs.

Young et al. (1989) reported that the hatchlings of *O. ornatus* are planktonic. Nothing is known of courtship or brooding behavior, and insufficient mature specimens are available to determine whether any seasonality to spawning exists.

Little information has previously been reported on the life history of *O. ornatus*. Houck (1982) reported that individuals of this species from Hawaii showed nocturnal activity patterns, with maximum activity between 2100 and 0200 hr. Active *O. ornatus* were observed foraging over reef flats or on sand and gravel substrata during night low tides. Captive individuals were found to enter deep, sleep-like inactivity during daylight hours, burrowing under gravel or sand during these light periods. Houck (1982) also reported that *O. ornatus* readily accepted grapsid crabs and shrimp species.

Discussion

The majority of the counts and indices recorded from the neotype fell within or close to the range observed in the Australian material, often close to the mean. The only marked exception was the index of hectocotylized arm length over the length of the opposite arm (OAI), which was much higher in the neotype than in the Australian material (OAI 84.7 versus 54.8–62.6–68.5 for the Australian material). The third left arm in the neotype was considerably shorter than in all other specimens examined, including Hawaiian material. The suckers on this are smaller in diameter than adjacent and opposite arms suggesting that the arm has partially regenerated from earlier damage. An additional Hawaiian specimen (USNM 214609) with intact arms had an OAI of 58.1. In Australian specimens, there is no well-marked long notch in the cutting edge of the upper beak, as reported by Voss (1981) for Hawaiian material.

Counts and indices were taken from additional specimens from Hawaii, Philippines, Fiji, Tahiti, Madagascar, Chagos Archipelago, Cook Islands and Aldabra Atoll. All possessed typical body morphology of long unequal arms, short webs, 13–14 gill lamellae and the characteristic pattern of white stripes and truncate flat papillae. Males possessed 144–171 suckers on the hectocotylized arm.

A number of cephalopod workers have recognized the distinct group of octopus species, often referred to as the *Octopus*

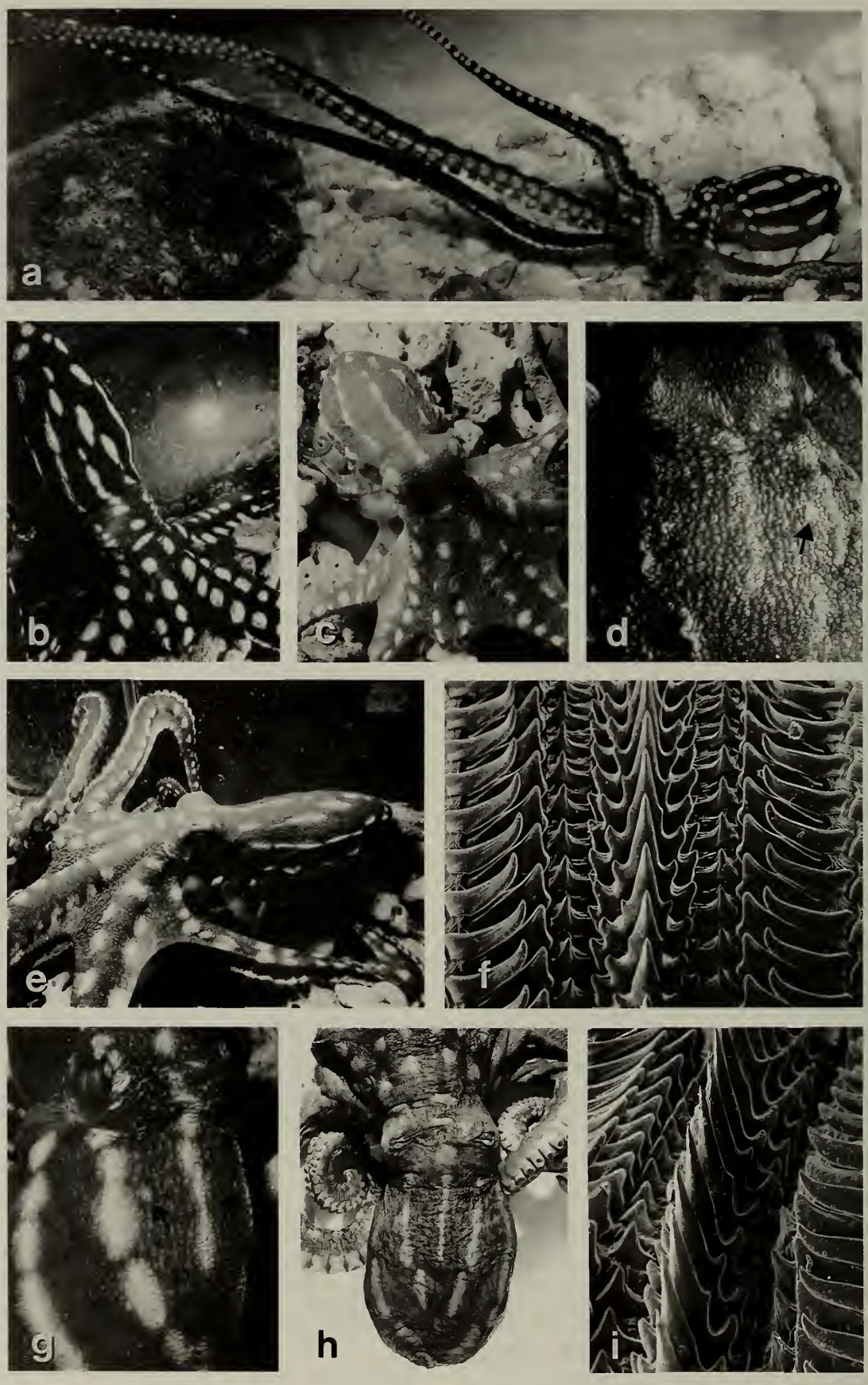

Fig. 4. *Octopus ornatus* Gould, 1852. a, Photograph of live animal (NMV F57920: 45.9 mm ML ♂); b–e, g Photographs of live animal (NMV F57918: 104.2 mm ML ♂); b, Dorsal mantle and arm crown showing darkened alarm coloration, Photo R. Fenwick; c, Dorsal mantle and arm crown showing raised flaps in white bars, Photo R. Fenwick; d, Dorsal mantle showing patch and groove system and dorsal white spots (arrows); e, Lateral mantle and arm crown showing raised flaps in white bars, Photo R. Fenwick; f, Scanning EM photograph of

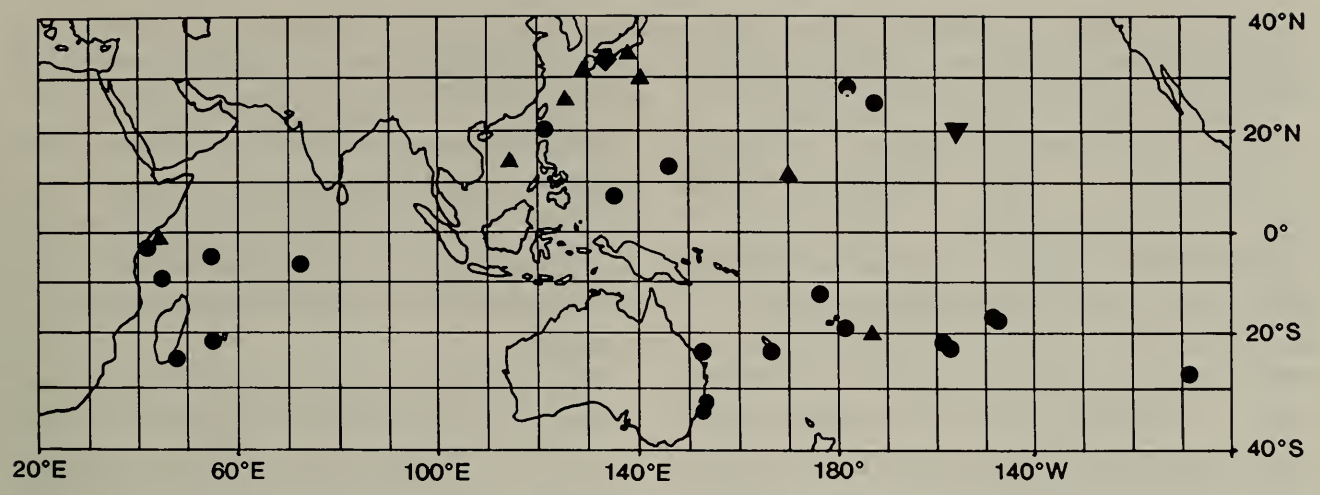

Fig. 5. Distribution of *Octopus ornatus* Gould, 1852. Symbols ▼ = type locality of *O. ornatus*, ◆ = type locality of *Callistoctopus arakawai* Taki, 1964, ● = material examined, ▲ = published records.

macropus group (Robson 1929, Adam 1941, Taki 1964, Voss 1981). These octopuses are characterized by elongate arms with dorsal arms always longest (arm formula typically 1.2.3.4), high gill counts (10–14 per demibranch), multicuspid radulae (rhachidian typically bears three lateral cusps on each side of a medial cone) and nocturnal activity patterns. *Octopus ornatus* exhibits all these characters and has been suggested to be a member of this group of species (Robson 1929, Adam 1941, Voss 1981).

Octopus ornatus often has been allied to the species from which this group receives its name, *O. macropus* Risso, 1826 (Gould 1852, Berry 1914, Robson 1929, Voss 1981, Roper & Hochberg 1988). The description and distribution of *O. macropus* s.s. currently are being reviewed by Hochberg, Mangold and Norman, who consider this species to be restricted to temperate waters of the Mediterranean and the north west African coast. Considerable geographic and temperature boundaries separate the distributions of *O. ornatus* from that of *O. macropus*. The two species are easily distinguished on the basis of color patterns, gill lamellae counts (13–14 for *O. ornatus* vs. 11–12 for *O. macropus*) and hectocotylized arm sucker counts (~160 for *O. ornatus* vs. ~110 for *O. macropus*).

The name, *O. macropus* Risso, 1826, regularly has been applied to elongate Indo-West Pacific octopuses with dorsal arms longest and high gill lamellae counts (10–14 per demibranch) [Joubin 1894, 1898; Goodrich 1896; Hoyle 1904; Berry 1912, 1914; Massy 1916; Wülker 1913, 1920; Odhner 1917; Robson 1926, 1929, 1932; Boone 1938; Adam 1939, 1942, 1946, 1954, 1959, 1960, 1973; Rees & Stuckey 1954; Voss 1963; Nesis 1982 (plate in 1987 translation); Roper, Sweeney, & Nauen 1984]. The restriction of the distribution of the true *O. macropus* to the Mediterranean and temperate Atlantic necessitates the need to critically review the Indo-West Pacific members of the *Octopus macropus* group. It also makes available a number of species names from the Indo-West Pacific which previously were synonymized with *O. macropus* (Robson 1929, Roper, Sweeney, & Nauen

←

radula from NMV F57918 (104.2 mm ML ♂); g, Dorsal mantle showing alarm coloration and position of dorsal white spots (arrows); h, Dorsal mantle of preserved specimen showing characteristic color pattern (NMV F57918: 104.2 mm ML ♂); i, Scanning EM photograph of radula from NMV F57918 (104.2 mm ML ♂) showing serial migration of lateral cusps on rhachidian tooth from lateral to medial position over 10–11 rows.

1984). The following nominal taxa show morphological and behavioral affinities with *O. ornatus,* yet are easily distinguished:

Octopus lechenaultii d'Orbigny, 1826 (and its synonym *O. cuvieri* d'Orbigny, 1826) were both described from Pondicherry in southern India. The holotypes of both nominal species were examined in Paris (*O. lechenaultii*: 1 ♀: 61.8 mm ML, MNHN 4-12-972; *O. cuvieri*: 1 ♂: 42.9 mm ML, MNHN 4-12-971). *Octopus ornatus* is distinct from this species with higher gill lamellae counts (13–14 for *O. ornatus* vs. 11–12 for *O. lechenaultii*) and more suckers on the hectocotylized arms (~160 for *O. ornatus* vs. 88 on the holotype of *O. lechenaultii*).

Octopus luteus Sasaki, 1929 was described from two types lodged in the Hokkaido Imperial University (110 mm ML male and 125 mm ML female), collected from the Pescadore Islands near Taiwan. *Octopus ornatus* is distinct from this species with longer arms (5.4–8.4 times ML in *O. ornatus* vs. 4–4.1 in *O. luteus*), more suckers on normal arms (>300 for *O. ornatus* vs. ~200 for *O. luteus*) and on the hectocotylized arm (~160 for *O. ornatus* vs. 88 on holotype of *O. luteus*), larger hectocotylus in mature males (4.3–5.7 for *O. ornatus* vs. 3.7 for *O. luteus*) and more gill lamellae (13–14 for *O. ornatus* vs. 12 for *O. luteus*).

Octopus nanhaiensis Dong, 1976 is known from a single male from Quangdong Province, China. It appears distinct from *O. ornatus* in possessing fewer gill lamellae (10 vs. 13–14). Additional material and access to the type material is required to clarify the status of this little-known species.

Octopus rapanui Voss, 1979 from Easter Island shows some similarities to *O. ornatus*. Specimens of both species collected from Easter Island were examined in the MNHN collection. These species can be distinguished easily by a number of characters. *Octopus ornatus* is distinct from this species having shallower webs [WDI 5.3–11.3 for *O. ornatus* vs. 18–23 for *O. rapanui* (Voss 1979)], more suckers on the hectocotylized arm [~160 for *O. ornatus* vs. ~105 for *O. rapanui* (MNHN specimens)], more gill lamellae [13–14 for *O. ornatus* vs. 11–12 for *O. rapanui* (Voss 1979)]; and distinguishing color patterns (deep maroon red with white longitudinal stripes and spots for *O. ornatus* vs. white base color with fine purple brown chromatophores on dorsal surfaces for *O. rapanui*).

Two species are known only from juvenile specimens. *Octopus taprobanensis* Robson, 1926 was described from a single juvenile of indeterminate sex (14.4 mm ML, BMNH 1925.11.23.2), collected from the Pearl Banks off Sri Lanka. It shows an arm formula of 1.2.3.4 and has 13–14 gill lamellae. *Octopus teuthoides* Robson, 1929 also was described from a juvenile of indeterminate sex (15.8 mm ML, BMNH 1928.3.28.1), collected from Vanuatu. It also shows the 1.2.3.4 arm formula and has 11 gill lamellae. Until the juvenile stages of members of the *Octopus macropus* group are resolved, it will not be possible to determine the status of these species.

Rochebrune proposed a new genus and species, *Eledonenta filholiana* Rochebrune, 1884, based on a male specimen from Fiji. Diagnostic characters for the genus were long arms with a single row of suckers. This perceived, single row of suckers led Rochebrune to place the genus in the Eledoninae Gray, 1849. The type specimen of this species was examined in Paris and is a poorly-fixed elongate specimen. The elongation of the arms appears to be an artefact of handling and/or fixation. There are two rows of suckers but arm elongation has spaced the suckers sufficiently for Rochebrune to interpret them as forming a zig-zag single row. Although poorly preserved, *E. filholiana* is clearly recognizable as a member of the *Octopus macropus* group. It has the typical arm formula of 1.2.3.4 and 10 gill lamellae. The status of this species needs resolution. *Octopus ornatus* is distinct from this species with higher gill counts (13–14 for *O. ornatus* vs. 10 for *E. filholiana*) and higher hecto-

cotylized arm sucker count (~160 for *O. ornatus* vs. 81 for holotype of *E. filholiana*).

Voss (1981) synonymized *Callistoctopus arakawai* Taki, 1964 with *O. ornatus*. Other works have reported *C.* (or *Octopus*) *arakawai* from Japanese and Chinese waters (Taki 1964, 1965; Dong 1979; Taki 1981; Dong 1987; Okutani, Tagawa & Horikawa 1987; Nishimura, 1992). Photographs, illustrations and descriptions provided in these works indicate the characteristic color pattern and morphology that identify these records as *O. ornatus*. The reports of *O. ornatus* from southern Japan (Taki 1964, 1965, 1981) are likely to be vagrant individuals carried north to the warm bays and inlets of southern Japan during their planktonic phase by the warm Kuroshio Current. This species does not, however, appear permanently established in the warm temperate waters of southern Japan.

Recent research into tropical Australian octopuses (Norman, 1991, 1992, 1993a, 1993b, 1993c) has resulted in the description of four new species (*O. alpheus, O. aspilosomatis, O. dierythraeus* and *O. graptus,* all Norman, 1993a). These octopuses exhibit characters typical of the *Octopus macropus* group; all share an arm formula of 1.2.3.4, moderate to high gill counts (10–14), multicuspid radula and nocturnal activity patterns. Full descriptions, and delineation of these species from *O. ornatus,* are presented in Norman (1993a).

The distribution of *O. ornatus* is expanded to include the east coast of Australia and the South Pacific Ocean (Fig. 5). New records within the known range also are reported from the Indian Ocean, Asia and the North Pacific Ocean. *Octopus ornatus* exhibits a distribution typical of shallow-water, wide-ranging, tropical Indo-West Pacific marine taxa. As reported for other biota exhibiting this range (Briggs 1974), the distribution of *O. ornatus* appears to be limited to waters within the 20°C winter isotherm.

The specimens of *O. ornatus* collected from the warm temperate waters of New South Wales probably result from planktonic juveniles carried south in the sporadic warm-water eddies of the East Australian Current. All were encountered on rocky shores of sheltered coasts, most in bays or inlets. Sporadic incursions of tropical species into temperate waters has been reported for many taxa (Bennett & Pope 1953, Wilson & Allen 1987). Bennett & Pope (1953) suggested that inlets and bays along the New South Wales coast can act as warm water refuges for tropical species, enabling tropical species to exist in such localities well south of their normal range.

Acknowledgments

This research forms part of a Ph.D. research program on octopods of the Great Barrier Reef and northern Australia, carried out in association with the Museum of Victoria and the University of Melbourne. Sincere thanks to F. G. Hochberg, M. Sweeney, C. C. Lu, C. F. E. Roper, T. Stranks and G. F. Watson for assistance with the manuscript and project; R. Fenwick and M. Turner for field assistance; I. Loch, P. Colman and B. Rudman (AMS), J. Stanisic (QMB), C. F. E. Roper and M. Sweeney (USNM), T. Gosliner and E. Kool (CASIZ), F. G. Hochberg and H. Chaney (SBMNH), F. Naggs (BMNH) and R. and G. Boucher-Rodoni (MNHN) for assistance and access to collections; S. Hochberg for kind hospitality and support; D. Paul and C. Rowley for assistance with photographic plates. This research was made possible through support grants from the Museum of Victoria, University of Melbourne, Victorian Institute of Marine Sciences, Australian Museum Postgraduate and Keith Sutherland Awards, Joyce W. Vickery Research Fund (Linnean Society of NSW), Ethel Mary Read Fund (Royal Zoological Society of New South Wales), Ian Potter Foundation, Hawaiian Malacological Society, Royal Society of Victoria, Western Society of Malacologists, and the Harkness Fellowships, Commonwealth Fund.

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Appendix.—*Octopus ornatus* Gould, 1852: material examined

Neotype: HAWAII: 1 ♂: 93.7 mm ML, USNM 730020, Oahu Island, Black Point (21°15′N, 157°48′W), coll. S. Kempf, 11 Jan 1976.

Australian material: QUEENSLAND: Capricorn Bunker Group, One Tree Island, 23°30′S, 152°05′E: 1 ♂: 45.9 mm ML, NMV F57920, reef channel, 2 m, coll. M. Norman, 15 Oct 1989 (1930 hr); 1 ♀: 77.3 mm ML, NMV F57919, reef channel, 2 m, coll. M. Norman, 3

Sep 1990 (0430 hr, in mouth of lair, flushed with $CuSO_4$); 1 ♂: 83.2 mm ML, NMV F57921, The Gutter, 0.2 m, coll. M. Norman, 4 Sep 1990 (0400 hr); 1 ♀: 83.5 mm ML, NMV F57922, The Gutter, 0.2 m, coll. M. Norman, 3 Sep 1990 (0215 hr); 1 ♂: 102.8 mm ML, NMV F57923, The Gutter, 0.2 m, coll. M. Norman, 3 Sep 1990 (0330 hr); 1 ♂: 103.5 mm ML, NMV F57924, reef channel, 0.2 m, coll. M. Norman, 4 Sep 1990 (0430 hr); 1 ♂: 104.2 mm ML, NMV F57918, The Gutter, 0.2 m, coll. M. Norman, 3 Sep 1990 (0215 hr); NEW SOUTH WALES: 1 ♂: 75.7 mm ML, AMS C115738, north of Sydney, Newport (33°39′S, 151°19′E), intertidal on rock platform, coll. I. Bennett, 27 Jul 1962; 1 ♂: 84.4 mm ML, AMS C156207, near Laurieton, Lake Cathie, 31°33′S, 152°5′E, coll. J. Ibbott, Mar 1977; 1 ♂: 97.1, AMS C115737, Sydney, Manly, Fairy Bower (33°47′S, 151°17′E), 19 Jun 1962 (in fish net); 1 ♀: 132.0 mm ML, AMS C169234, off Tuncurry (32°47′S, 151°29′E), coll. J. C. Moore, 1965.

Other material: VATAO ISLAND: 1?: 11.0 mm ML, USNM 817781, 19°48′S, 178°15′W, 4.6–9.1 m, coll. V. G. Springer, stn. 86, 14 Jun 1986 (poison station); FIJI: 1?: 17.1 mm ML, USNM 817782, Rotuma, east end of Malaha, north coast, 12°30′S, 177°05′E, 0–1.8 m, coll. V. G. Springer, ca. 15 May 1986 (rocky (lava) shore with some sand and coral rubble, rotenone station); 1?, 1 ♂: 17.1, 51.1 mm ML, USNM 817641, north east corner of Rotuma, just west of wharf, 12°30′S, 177°05′E, 10.5 m, coll. V. G. Springer, 12 May 1986 (isolated reef patch, mostly dead coral rocks, rotenone station); PHILIPPINES: 1?, 1 ♂: 22.5, 44.4 mm ML, USNM 817642, Batanes, Batan Island, White Beach past Mahatae, 20°24′45″N, 121°55′02″E, 0–6 m, coll. D. Johnson, 22 Apr 1987 (surge channel at outer edge of reef, rotenone station); PALAU ISLANDS: 1 ♀: 22.9 mm ML, CASIZ 031970, Angaur Island, Gangaraoi (6°55′N, 134°09′E), coll. De Witt, 22 Oct 1957; CHAGOS ARCHIPELAGO: 3 ♀: 23.0–38.4 mm ML, USNM 817640, Eagle Island, 6°10′45″S, 71°21′32″E, 0.5–1 m, coll. R. Winterbottom, 27 Nov 1979 (1015–1230 hr, tidal flats and channels, low tide, rotenone); 1 ♀: 87.0 mm ML, BMNH unreg., Peros Banhos, Ile du Coin, off Jetty (5°18′S, 72°00′E), 6 m, coll. A. Shepherd, Joint Services Chagos Expedition 1978, Mar 1979 (Acc. No. 2307); HAWAII: 1?: 26.7 mm ML, USNM 817783, Waianae (21°26′N, 158°11′W), coll. USBCF, Honolulu, 1 Jul 1951 (2100–2230 hr, attracted to night light); 1 ♂: 27.9 mm ML, USNM 817784, Midway Island (28°12′N, 177°24′W), coll. USBCF, Honolulu, Jul or Aug 1955 (attracted to night light); 1 ♂: 31.8 mm ML, CASIZ 021564, Oahu, Honolulu Reef (21°30′N, 158°00′W), coll. USS *Albatross,* 1902 (Berry voucher specimen SSB#179, CASIZ holotype no. 506); 1 ♀: 43.4 mm ML, CASIZ 034975, Leeward Islands, Laysan Island, west side on reef, 25°46.3′N, 171°44.7′W, coll. R. R. Harry, 27 Jun 1951; 1 ♀: 45.8 mm ML, CASIZ 035015, east of Laysan Island, anchorage off Aro Reef, 25°25.5′N, 170°41.5′W, coll. R. R. Harry, 5 Jul 1951; 1 ♂: 73.8 mm ML, USNM 817787, 21°15′N, 157°44′W, *Albatross* surface tow net survey, serial no. 286, 2 Dec 1891 (1700 hr, caught at surface; 1 ♂: 79.4 mm ML, CASIZ 034977, Oahu, Honolulu Fish Market (21°30′N, 158°00′W), coll. D. S. Jordan and Joseph Grinnell (from Stanford collection); 1 ♂: 88.1 mm ML, USNM 214609, Oahu, Honolulu Market, 21°20′N, 157°55′W, *Albatross* cruise, between 1902 and 1914; REUNION ISLAND, 1?: 26.9 mm ML, NMV F60139, (21°06′S, 55°36′E), coll. M. Jay, MNHN, 1991 (station N2); ALDABRA ATOLL: 1 ♂: 30.8 mm ML, MNHN 4.7.923, Aldabra Island (10°30′S, 46°30′W), 1954; 2 ♂, 2 ♀: 51.9–121.0 mm ML, USNM 817638, West Island, 9°22.8′S, 46°12.4′E, 0.75 m, coll. H. A. Fehlmann, 14 Aug 1967 (1700–1900 hr, on sand and coral rubble, rotenone); SOCIETY ISLANDS: 1 ♂, 2 ♀: 37.3–58.0 mm ML, NMV F30256, Tahiti, Teahupo Presquile de Taiarapu (17°51′S, 149°15′W), 0.1 m, coll. R. Boucher, 18 Mar and 1 Apr 1972 (rubble bottom in lagoon at night); unmeasured, USNM 575419, Raiatea, Uturoa, station 77, (16°44′S, 151°25′W), 0.3 m, coll. H. A. Rehder, 28 Apr 1957 (muddy sand flat east of church and school, swimming); unmeasured, USNM 576016, Tahiti, Taone (17°30′N, 149°30′W), coll. R. Sixberry; COOK ISLANDS: 1 ♂: 38.0 mm ML, CASIZ unreg., Ka'umata, Majaia, 21°54′30″S, 157°58′00″W, coll. Vanderbilt Foundation Cook Islands Expedition, 25 May 1958; 1 ♂: 44.1 mm ML, CASIZ 034026, Manaia, 21°54′30″S, 157°58′00″W, coll. D. S. Marshall; 1 ♀: 85.2 mm ML, USNM 817639, Raratonga, Arorangi (21°13′S, 159°49′W), coll. G. Paulay, 14 Oct 1984 (on fringing reef, swimming at night); MADAGASCAR: 1 ♂: 67.2 mm ML, SBMNH 64492, Libanona Beach, Taolanaro (Fort Dauphin), 25°02′S, 47°00′E, coll. Henry W. Chaney, 23 Mar 1990 (active on reef terrace amongst tidepools and algae, intertidal at night); MARIANA ISLANDS: 1 ♀: 72.5 mm ML, CASIZ 031971, Guam, 0.5 mile SW of Agat Village, sand flat off north side of Bangi Point, 13°22′36″N, 144°38′53″E, coll. Fehlman, 12 Oct 1958; EAST AFRICA: 1 ♂: 85.0 mm ML, USNM 817778, Kenya, Mombasa Fish Market (4°04′S, 39°40′E), coll. J. C. Miguel, 11 Feb 1979 (purchased at market); SEYCHELLE ISLANDS: 1 ♂: 92.1 mm ML, MNHN 4.4.880, (4°30′S, 55°30′E), rec. Dussumier, 1830; EASTER ISLAND: 1 ♂: 96.1 mm ML, MNHN 3.12.784, (27°05′S, 109°20′W); 1 ♀: 104.3 mm ML, MNHN 3.10.753, (27°05′S, 109°20′W).